

**NANOWANA GEN. NOV., SMALL MADTSOIID SNAKES
FROM THE MIOCENE OF RIVERSLEIGH: SYMPATRIC SPECIES
WITH DIVERGENTLY SPECIALISED DENTITION**

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Two small early Miocene madtsioid snakes from Riversleigh, NW Queensland are described as *Nanowana godthelpi* gen. et sp. nov. and *N. schrenki* gen. et sp. nov. Jaw elements of the former are depressed, lack ankylosed teeth, and have alveoli of nearly uniform size, these features are interpreted as signs of a coadapted character complex ('arthrodonty') where the teeth are attached to the jaws by a fibrous hinge. This condition is associated with a diet of hard-scaled scincid lizards. The latter species retains ankylosis, and has strongly enlarged teeth on the anterior dentary and middle maxilla indicating a distinct method of subduing prey, but extant analogues are also predominantly scineivorous. Departure in each species from the nearly homodont, ankylosed condition in other madtsioids is interpreted as adaptation to a diet of scincid lizards. These divergent, but functionally parallel specialisations are likely to be independently derived from the ancestral condition.

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Madtsioid snakes in Tertiary faunal assemblages of Riversleigh (Scanlon 1992, 1993, 1995, 1996) have been referred to *Yurlunggur* Scanlon, 1992 and *Wonambi* Smith, 1976. Other Riversleigh madtsioids cannot be included in previously known genera. Two small species, estimated to reach 1m long, are represented by upper and lower jaw elements from System B (Archer et al., 1989, 1994) on Godthelp Hill. Some are associated with vertebrae, but the two species cannot be distinguished unambiguously on vertebral characters. I include them in a single genus which possibly unnatural treatment allows generic identification of isolated vertebrae from other sites.

This paper provides descriptions of the two species including some ontogenetic stages. While analysis of phylogeny of madtsioids awaits detailed comparisons with other primitive snakes, some functional and evolutionary points are noted by analogy with extant forms.

MATERIALS AND METHODS

Material is housed in the Queensland Museum (QMF), Australian Museum (AMF), Northern Territory Museum of Arts and Sciences (NTMP), Museum of Victoria (NMVP), and South Australian Museum (SAMP). ... (SMNR) specimens examined in Paris by courtesy of J.-C. Rage.

Teeth or alveoli are numbered beginning from the anterior on complete jaw elements; on fragments where the tooth row is or may be incom-

plete anteriorly the numbers are spelled out in words. In illustrating cranial bones, views of the same specimen are usually arranged parallel to each other, in lateral, dorsal, medial, ventral aspects. Figures of vertebrae have left lateral, anterior, posterior, dorsal, and ventral views of each element in a vertical row. If more than one vertebra are shown in an illustration, they are arranged (l to r) in order from anterior to posterior.

SYSTEMATICS

Family MADTSOIIDAE Hoffstetter, 1961

Nanowana gen. nov.

TYPE SPECIES. *Nanowana godthelpi* sp. nov.

OTHER SPECIES. *Nanowana schrenki* sp. nov.

ETYMOLOGY. Greek *nanos*, a dwarf and Warlhirri (Tanami Desert, central NT) *Wana*, Rainbow Serpent of Aboriginal mythology.

DIAGNOSIS. Small, upto 1.5m long; neural spine low to moderately high, not extending close to anterior edge of zygosphenes; zygosphenes shallow, with anterodorsal edge straight, slightly convex or concave in dorsal view; subcentral ridges well-defined, straight or slightly concave or convex in ventral view; haemal keel relatively narrow, with 'paired hypapophyses' in posterior trunk defined laterally, but not projecting ven-

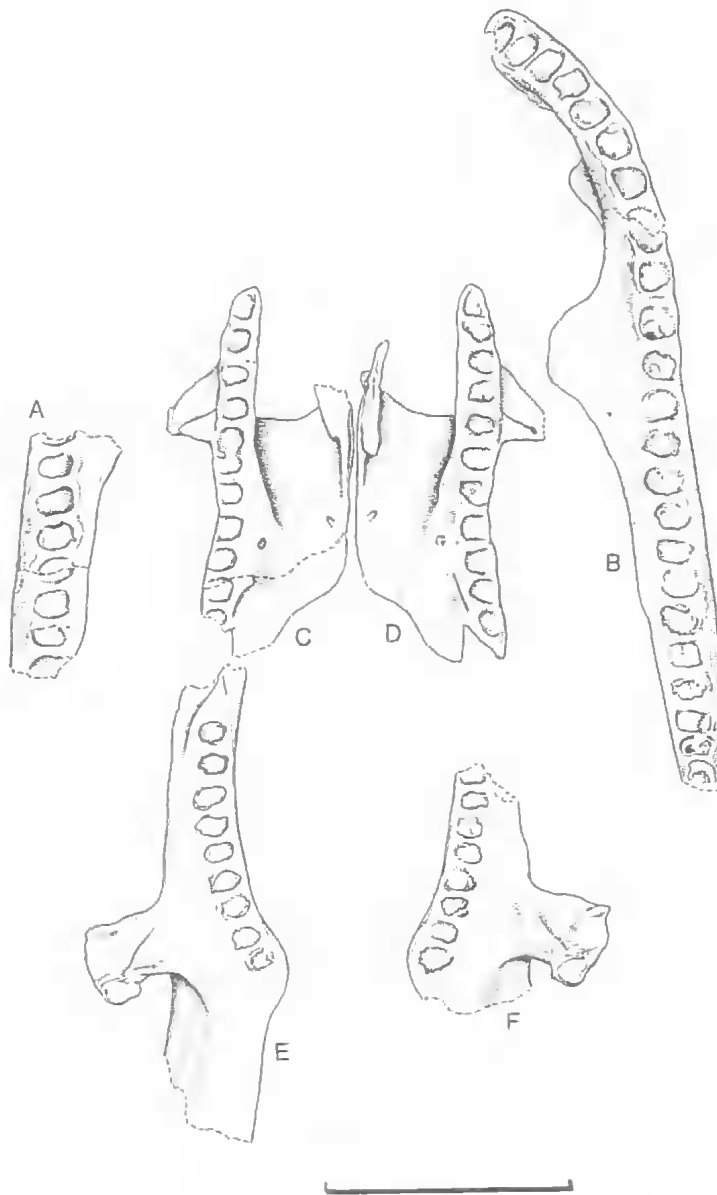


FIG. 1. *Nanowana godthelpi* sp. nov., QMF31379, holotype, upper jaw bones (right (A) and left (B) maxillae, palatines (C,D) and pterygoids (E,F) of a single individual) in palatal view, CS Site. Scale bar=5mm.

trally or separated by a median concavity; neural arch in posterior trunk depressed, its lateral portions strongly concave dorsad. Anterior tip of maxilla with medial expansion (septomaxillary process) contributing to floor of narial chamber;

dorsal process with steep anterior edge; dentary with at least 2 mental foramina.

COMPARISON. This genus is distinguished from all madtsoiids other than *Alamitophis* by the zygosphene in dorsal view frequently (but not always) having a convex anterior margin; the convexity is broad rather than a distinct median tubercle as in *Alamitophis*. It is distinguished from *Yurlunggur*, *Wonambi*, *Rionegrophis*, *Gigantophis* and *Madtsoia* by being smaller. Its neural spines are lower, at corresponding positions in the trunk, than in *Madtsoia*, *Rionegrophis*, *Wonambi* and *Alamitophis*, but higher than *Patagoniophis* or *Gigantophis*. It is distinguished from all genera except *Patagoniophis* by the less steeply converging subcentral ridges (relatively more elongate centrum in ventral view). Maxillae resemble *Madtsoia* sp. (SMNR 2879, Itaborai) and are distinguished from *Wonambi* and *Yurlunggur* by prefrontal process having a steep anterior edge; distinguished from each of these by development of the septomaxillary process (condition unknown in other madtsoiids).

DISCUSSION. Vertebrae can be distinguished from other madtsoiids, but their common features (including small size) may be symplesiomorphic; the concept of *Nanowana* containing these 2 species can be described as a 'marriage of convenience'. The phylogenetic relationships of these with other madtsoiids remain unknown, but they are treated as a unit because their vertebrae (which provide

the only taxonomically useful material in most deposits) are unable to be distinguished in many cases.

In a number of aspects of the vertebrae, including size, *Nanowana* is comparable to *Patagoniophis* sp. cf. *P. parvus* from the early Eocene Tingamarra Local Fauna (Scanlon 1993); differences include the higher neural spine (in adults), narrower haemal keel in the posterior trunk, frequently convex anterior edge of the zygosphenes, and dorsolateral concavities of the posterior neural arch. It differs from *Alamitophis*, which also occurs in the Australian Eocene (Scanlon, 1993): the anterior edge of the zygosphenes, when convex, is broadly so rather than forming a distinct prominence; paradiapophyses do not project anteriorly; zygapophyses are more steeply inclined at equivalent positions within the column. The lower neural spine, broader zygosphenes, and features of the haemal keel or hypapophyses differentiate *Nanowana* from *Wonambi* Smith, (1976) (*Wonambi* is known from Riversleigh, much smaller than *W. naracoortensis* but larger than *Nanowana*; Scanlon, 1996).

The only other known Australian madtsoiid is *Yurlunggur*, at least 2 species of which occur at Riversleigh as well as the type species from Bullock Creek (middle Miocene; Scanlon 1992). That genus exceeded 5m and thus included only 'giant' snakes, though not as large as *Gigantophis garstini* or *Madtsoia bai*. However, size is rather variable in many snake genera (e.g. the pythonid *Morelia*, sensu Underwood & Stimson, 1990, includes species with maximum

lengths from under 1m to over 7m), and need not be considered an essential part of the diagnosis. The vertebrae of small and large forms are rather similar except in features which may be directly related to size (neural spine height is variable

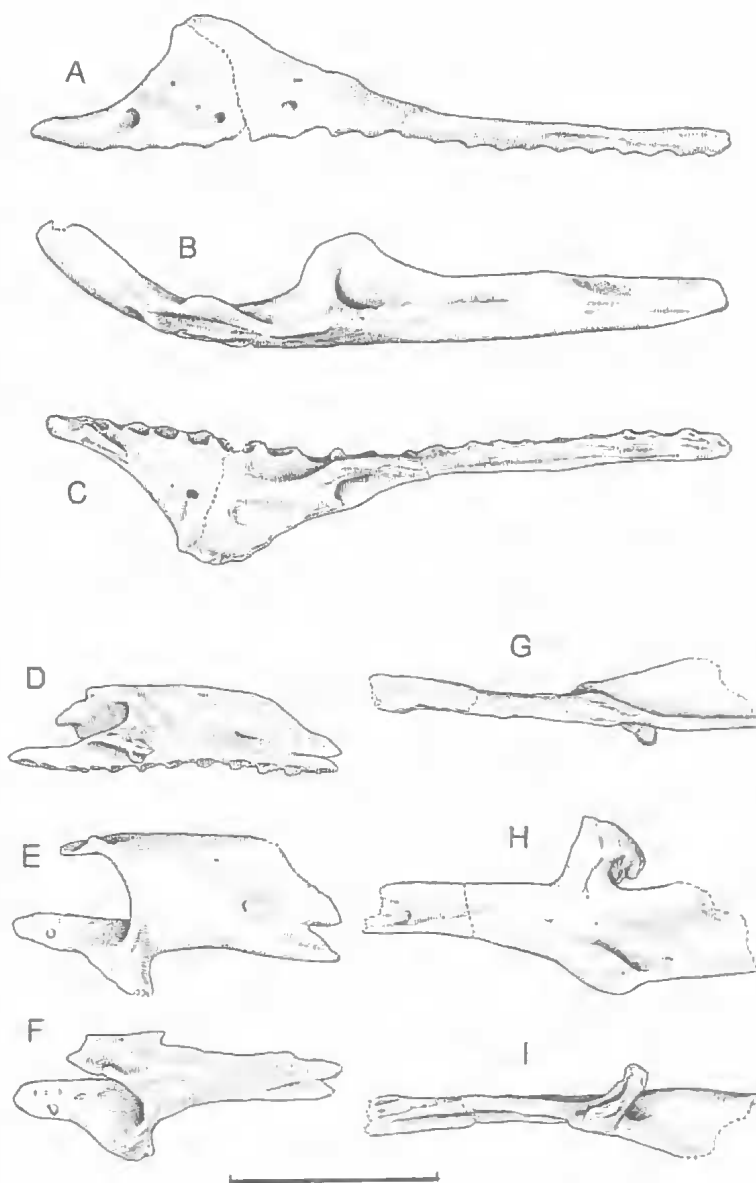


FIG. 2. *Nanowana godthelpi* sp. nov. QMF31379, holotype, upper jaw bones (left maxilla (A-C), left palatine (D-F) and right pterygoid (G-I)) in lateral, dorsal and medial views, CS Site. Scale=5mm.

within *Yurlunggur*, and is proportionally similar to *Nanowana* in some), but *Nanowana* differs from *Yurlunggur* in the shape of the zygosphene, and the haemal keel of posterior trunk vertebrae being narrower and lacking a median concavity.

Comparisons with non-Australian forms do not suggest any links closer than that with *Yurlunggur*, and will not be pursued here. The rib-heads of *Nanowana* have not been considered in detail, but appear to be similar in shape to those of *Yurlunggur* and *Wonambi* (Scanlon, 1993).

***Nanowana godthelpi* sp. nov.**
(Figs 1-8, Table 1)

ETYMOLOGY. For Henk Godthelp, University of New South Wales, in recognition of his contributions to Australian palaeontology.

MATERIAL. Holotype QMF31379, associated elements of a single individual comprising partial to complete maxillae, palatines and pterygoids of both sides. Paratypes QMF31383, 31384 associated dentaries and compounds of a single individual; dentaries QMF20892, 23052, 23053, 23054, 23056; maxillae QMF31380, 31382, 31386, 31387; palatine QMF31381; pterygoids QMF23058, 31393. All types from early Miocene (System B) Camel Sputum Site, Godthelp Hill. Other material: Camel Sputum Site, trunk vertebrae QMF19741. Upper Site, dentary QMF31389; palatine QMF23066; maxilla fragment QMF31390; pterygoids QMF23067, 31385; series of cloacal vertebrae. Mike's Menagerie Site, anterior fragment of pterygoid QMF19742. Creaser's Ramparts Site, dentary QMF23076.

DIAGNOSIS. Palatine lateral process about as long as two alveoli (nearest to 4th and 5th), ventral concavity of process with obtuse angle accommodating posterolateral angle of palatine process of maxilla. Maxilla with 23 tooth positions, palatine 11, pterygoid 9, dentary 16. Teeth not ankylosed to alveoli; maxillary alveoli vary only slightly in size, dentary alveoli largest in centre of tooth row (4-8 or 5-8). Posterior part of maxilla strongly depressed. Dentary tooth row curved in dorsal view. Two or 3 mental foramina, all anterior to the 7th alveolus.

DESCRIPTION OF HOLOTYPE. Upper dentigerous elements in a single block (without vertebrae or other elements) are complete on one or both sides, missing bilaterally only the posterior (quadrate) processes of the pterygoids (Figs 1,2). Maxillae long and flat posteriorly, supporting a high lizard-like prefrontal process anteriorly; palatines with 'alethinophidian' features; pterygoids

with prominent, also lizard-like, ectopterygoid processes. Proportions of jaws indicating a relatively long postorbital skull and moderately short, rounded snout.

Palatine: Left more complete than right, both well-preserved. Eleven alveoli forming a sigmoid tooth row, convex laterad anterior to an inflection and lateral concavity (slight, but definite and angular) between 7th and 8th. Dorsolateral crest arising above 3rd alveolus, bifurcating above 4th to form anterior edges of maxillary and choanal processes. Maxillary process with an oblique anterior edge (near 45° from sagittal plane), longitudinal lateral edge and transverse posterior crest on its ventral face, level with the 5th alveolus on the left palatine (4th-5th on right side); process not perforated or notched for the maxillary nerve. Anterior edge of the choanal process smoothly concave anteriorly for its full width, reaching between level of 4th and 5th alveoli; then curving strongly anteroventrally, extending to front of 2nd alveolus. Vertical anteromedial part of the choanal process bilobed anteriorly, a dorsal lobe curved mediad, the other laterad (forming articulations with the parasphenoid and vomer); third, posterolaterally pointed, lobe on the ventral edge deflected laterad, contributing (along with the vomer and ectochoanal cartilage, presumably) to the floor of the choanal passage. Lamina of choanal process strongly arched anteriorly, flatter posteriorly, and ventrally deflected part of lamina reducing in depth posteriorly. Posteromedial corner of process level with rear of 9th alveolus, posterior margin sinuous so that posterior process not sharply demarcated (as in some specimens); margin concave medially, convex posteriorly. Posterior extremities of choanal process and tooth row extending back level with each other, both with lateral margin parallel to tooth row, and separated by a distinct triangular notch extending forward to middle of 11th alveolus (thus, posterior edge W-shaped); on dorsal face this notch continued as a tapering trough extending to rear of 9th; ventrally a step-like groove running from the apex of the notch anteromedial to between 9th and 10th, with a shallow trough posterior and partly medial to the groove. Small foramen dorsomedially on the dentigerous process, just below the ridge continuous with the anterior edge of the choanal plate; a large foramen medial to the 8th alveolus, piercing the plate and emerging dorsally as a posteriorly widening foramen between 8th and 9th; another small foramen anteromedial to 10th alveolus. Dorsomedially on the anterior dentigerous process with tip of a tooth

emerging from the bone (this is the only tooth associated with jaws of this species).

Right and left palatines almost identical; spacing of alveoli slightly different on different sides; alveoli 2-5 in the right shifted posteriorly, relative to the left (alveoli 1 and 2 on the left, 5 and 6 on the right, confluent). Lateral (maxillary) process with small but distinct angular concavity marking the longitudinal (lateral) and oblique (anterolateral) sections of the margin.

Pterygoid. Nine alveoli (complete row), anterior tip (length of approximately 1.5 alveoli) edentulous. Tooth row curving medially posteriorly, following inner edge of bone; ventral face narrowing to a point anterior to tooth row, point interlocking with posterior notch of palatine. Dorsal surface forming a longitudinal trough, with foramen above 1st alveolus (opening anteriorad), lateral to a dorsomedial ridge. Lateral margin smoothly convex, diverging gradually from tooth row; anterior edge of ectopterygoid process diverging at about 120° from this margin, level with 7th alveolus. Process nearly as wide as rest of bone at this point, about as long as wide; its anterior and lateral edges at 90° in dorsal or ventral view, lateral margin inclined strongly posteroventrally, with posterior extremity produced as a knob-like extension, and posterior edge strongly concave. No part of the ectopterygoid facet exposed dorsally. Concave posterior surface of the process continuous with the ventrolateral face of the posterior lamina (quadrate process), bounded

medially by a narrow extension of the ventral (occlusal) surface. Quadrate process broken off

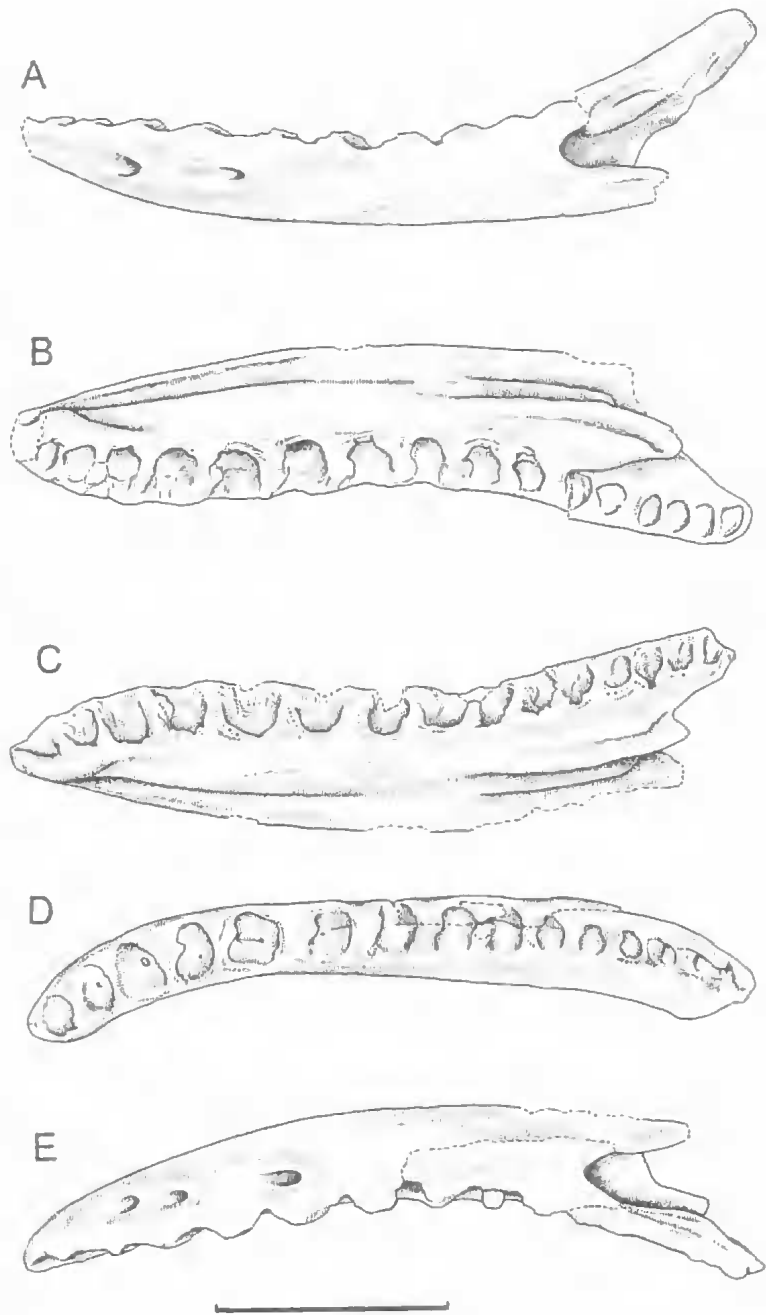


FIG. 3. *Nanowana godthelpi* sp. nov. QMF31383, 31384, paratype lower jaws. A, B, left dentary in lateral and medial view (upper posterior process broken and slightly displaced). C, D, E, right dentary in medial, dorsal, and lateral view. Scale=5mm.

TABLE 1. Measurements (mm) of jaws of *Namowana godthelpi* sp. nov. C1, C2, etc.=single individuals; L=left, R=right. Alveoli were selected as landmarks for some measurements because they could be identified in fragments, but there is variation in the position of anterior alveoli (even between sides of an individual). Values in brackets are minima for measurements affected by damage.

Palatine (ventral view): ptl=length of palatine from anterior tip of dentigerous process to posterior tip of tooth row spine or choanal process; pcl=base length of choanal process from intersection of anterior edge with dentigerous process to apex of posterior notch; pl 11=length from anterior tip to anterior edge of 11th alveolus; ptw=width across choanal and maxillary processes; pcw=width in same line of choanal process; prw=width in same line of tooth row bar; pmw=width in same line of maxillary process.

Pterygoid (ventral view): ttl=length from anterior spine (in plane of alveoli, not dorsal lappets) to rear of 9th alveolus; trl=tooth row 1st-9th alveolus; tte=from anterior spine to furthest point of ectopterygoid process; tl5=length across most posterior 5 alveoli (5-9); taw=width between near-parallel edges anterior to ectopterygoid process; tpw=width from basipterygoid facet to intersection of ectopterygoid process and dorsolateral edge of posterior lamina; ttw=width from basipterygoid facet to furthest point of ectopterygoid process.

Maxilla: mtl=length; map=length from anterior tip to posteromedial angle of palatine process; m 712=length from anterior edge of 7th-13th alveolus; mpw=width across palatine process; mph=depth at prefrontal process.

Dentary: mff=number of mental foramina; dtl=straight-line length; dl 15=length to anterior tip of 15th alveolus; dl f=length to lateral fossa; d4t= posterior edge of 4th alveolus to posterior extremity; d4 15=posterior edge of 4th to anterior edge of 15th; d4f= posterior edge of 4th to lateral fossa; dl 7=anterior tip to anterior edge of 7th alveolus; dmd=depth from dorsolateral to ventromedial edge in middle part of bone; dpp=depth of upper posterior process.

QMF	31379		31381	23058	31386	31380	31382	31393	23066	23067	31385
Ind.	C1 R	C1 L	C2 L	C2 L	C2 R	C3 R	C3 L	C4 R	U1 L	U1 R	U1 L
ptl	(7.6)	7.7	(8.0)	-	-	-	-	-	-	-	-
pcl	4.4	4.2	4.0	-	-	-	-	-	4.5	-	-
pl11	6.6	6.7	6.8	-	-	-	-	-	-	-	-
ptw	3.9	(3.8)	4.0	-	-	-	-	-	3.8	-	-
pcw	1.9	1.9	2.0	-	-	-	-	-	2.0	-	-
prw	0.9	0.9	1.1	-	-	-	-	-	1.0	-	-
pmw	1.1	(1.0)	(0.9)	-	-	-	-	-	(0.8)	-	-
ttl	5.7	-	-	-	-	-	-	-	-	-	-
trl	4.9	-	-	-	-	-	-	-	-	-	-
tte	6.8	-	-	-	-	-	-	-	-	-	-
tl5	2.6	2.5	-	3.2	-	-	-	1.6	-	3.1	3.0
taw	1.7	1.6	-	1.7	-	-	-	(1.0)	-	1.6	1.6
tpw	2.4	2.4	-	3.1	-	-	-	-	-	2.9	3.0
ttw	4.2	4.1	-	(3.9)	-	-	-	-	-	4.3	(3.9)
mtl	-	(16.3)	-	-	-	-	-	-	-	-	-
map	-	7.4	-	-	-	-	-	-	-	-	-
m712	-	5.4	-	-	5.7	4.6	5.2	-	-	-	-
mpw	-	2.3	-	-	(2.8)	2.8	2.8	-	-	-	-
mph	-	(3.3)	-	-	3.9	3.6	3.3	-	-	-	-
Dentaries											
QMF	31383	31384	20892	23052	23053	23054	23056	31389	23076		
Ind.	C1 R	C1 L	C2 L	C2 R	C3 L	C3 R	C4 R	UIL	CRL		
mff	3	2	2	3	2	-	2	3	-		
dtl	-	-	-	15.1	-	-	-	-	-		
dl15	15.6	-	14.1	13.3	-	-	-	-	-		
dlf	12.3	-	11.4	11.2	-	-	-	12.4	-		
d4t	-	13.6	-	11.9	-	-	-	-	16.3		
d415	11.3	12.3	11.1	10.2	-	-	-	-	14.2		
d4f	8.0	9.5	8.2	8.2	-	7.7	4.9	9.6	11.0		
dl7	7.8	-	6.5	6.3	8.0	-	-	-	-		
dmd	3.2	3.0	2.7	2.6	3.3	(2.4)	1.6	2.9	(2.6)		
dpp	1.0	0.9	0.9	0.9	-	-	-	-	1.4		

posteriorly about half the length of the tooth row behind the ectopterygoid process. Basipterygoid articular surface opposite ectopterygoid process, an oval facet facing dorsally and slightly medially, beginning level with front of 8th alveolus and extending to beyond 9th, only slightly distinct in outline from the rest of the medial edge. Apart from the anterior foramen mentioned above, 3 foramina dorsally, anterior, lateral and posterior to the facet; anterior 2 near the midline of the bone, posterior foramen close to the medial edge. A shallow but distinct transverse groove on the dorsal surface of the ectopterygoid process.

Left pterygoid retaining posterior 8 alveoli, which are slightly smaller and more closely spaced than on the right; possibly a 10th alveolus or longer edentulous gap anteriorly.

Maxilla. Alveoli 23, varying only slightly in size; row curved medially anteriorly, straight posteriorly. Anterior alveoli elongate anterolateral-posteromedially; anterior of maxilla wider than deep, with dorsomedial edge forming a crest above 1st-3rd alveoli, with slight concavities dorsal and medial to it. In lateral view, ventral margin slightly convex up to 10th alveolus, nearly straight posteriorly; dorsal edge rising smoothly and increasingly steeply from the anterior tip to between 6th and 7th alveoli; highest part of the dorsal process (7th to 9th) forming the dorsomedial surface for articulation with the prefrontal. On the posterior slope of the process, a low prominence above the 11th alveolus probably the insertion site for the postorbital ligament, but may also mark the anterior extent of the jugal; by 13th bone very shallow, continuing so to the posterior extremity. Large lateral (trigeminal) foramen opening anteriorly above the 5th-6th alveoli; two smaller foramina, equally close to ventral edge, above 7th-8th and 9th-10th, and 3 small foramina higher on the prefrontal process. Medial edge forming a shelf-like 'septomaxillary' process from 2nd to 4th alveolus, separated from the palatine process which widens gradually from 7th and then sharply at 10th, then gradually approaches maximum width at a sharply obtuse posteromedial angle between 11th and 12th. Medial shelf narrowing steeply from this point, then very gradually, but with a step-like inflexion at level of 18th alveolus (marking location of anterior tip of ectopterygoid). Large foramen entering maxilla at broadest part of the palatine process, above 11th alveolus, and a smaller foramen exits at the same level above the 7th. Tooth row following lateral margin closely from 1st-11th alveoli, then gradually crossing over with 19th-23rd

closer to medial edge; lateral edge forming a low dorsolateral crest (possibly homologous with more prominent crests or bulges in snakes such as *Dinilysia* and pythons). Lateral as well as medial parts of posterior maxilla apparently overlapped by the ectopterygoid, forming slight concavities on either side of a slight dorsal crest. Between ectopterygoid facet and prefrontal process, the suborbital surface with a shallow longitudinal groove which probably either was, or bounded, a facet for the jugal (an element lost in extant snakes but probably retained in *Dinilysia* and madtsoids, including *Wonambi*; Estes et al., 1970; Scanlon, 1996).

PARATYPES. Right and left mandibles (QMF31383, 31384), each compound and dentary, in loose articulation, lacking the splenial, angular and coronoid of each side (Figs 3, 4).

Right: Tooth row incomplete posteriorly, broken through 15th alveolus; no sign of ankylosed teeth. 4th to 8th largest alveoli, subequal, size reducing posteriorly and anteriorly. In lateral view, dorsal edge convex dorsad from 1st to 5th alveolus, concave dorsad for rest of length. Ventral edge slightly concave anteriorly, remainder convex but somewhat worn. Three mental foramina, below 3rd, 4th and 6th alveoli, opening anterodorsad. Posterior lateral fossa (compound notch) extending to between 10th and 11th. Lateral face smooth but with dorsolateral ridge defined by slight longitudinal concavity through foramina. In dorsal view, tooth row concave mediad, slightly more so anteriorly; alveoli round or squarish except first two which are somewhat elongate transversely. 15th alveolus on a narrow process distinguished by an angular concavity from the expanded dorsomedial shelf. The medial ridge forming the upper edge of Meckel's groove overhanging the groove distinctly up to the 8th alveolus; the overhanging edge of the upper facet for the splenial beginning below the 8th but more dorsally, forming with a slightly acute, pointed posteroventral process separated by a right-angle notch (in medial view) from the dorsal shelf. Meckelian groove narrowing anteriorly, anterior end slightly expanded, communicating by a foramen with alveolus of 1st tooth. Smooth bulb-like swelling overhanging the groove medial to the 1st and 2nd alveoli.

Left: Two mental foramina, between 3rd and 4th, and 5th and 6th. Posterior lateral fossa extending to between 11th and 12th alveoli.

Right compound. Elongate, shallow, 18.8mm long, 16.8mm from anterior tip to dorsal extrem-

ity of articular facet. Surangular lamina low but concave above, forming low coronoid process posterior to articulation with dentary, about 1/3 of length from anterior tip. Maximum depth of compound less than depth of dentary at articulation (suggesting that the coronoid extended dorsal to compound, forming most of the coronoid process by itself). Ventral edge, and lateral in dorsal view, nearly straight, but posterior end (below articular facet and retroarticular process) deflected slightly ventrad and mediad from main shaft. Articular facet dorsal and medial in position, not extending to lateral face, reaching to middle of medial face, and as far anterior as ventrad from dorsal extremity; facet defined posteriorly by a raised transverse lip, followed by a groove anterior to the sigmoid dorsal edge of the retroarticular process. Slight ventrolateral and deeper ventromedial concavities defining a ventral ridge on the retroarticular process. Shaft of compound nearly cylindrical just anterior to articular facet; a small dorsolateral foramen in this region. Mandibular fossa narrow, beginning posteriorly at level of foramen, curved slightly mediad, and extending to half way between posterior edge of coronoid facet and top of coronoid process.

Fossa partly surrounded by the facet for the coronoid anteriorly; anterior half opening below into mandibular foramen. Surangular lamina curved, overhanging the mandibular fossa for most of its length; reducing in height anterior to coronoid process in two steps, reaching a horizontal or somewhat dorsally concave shelf receiving the posterior part of the dentary; lateral

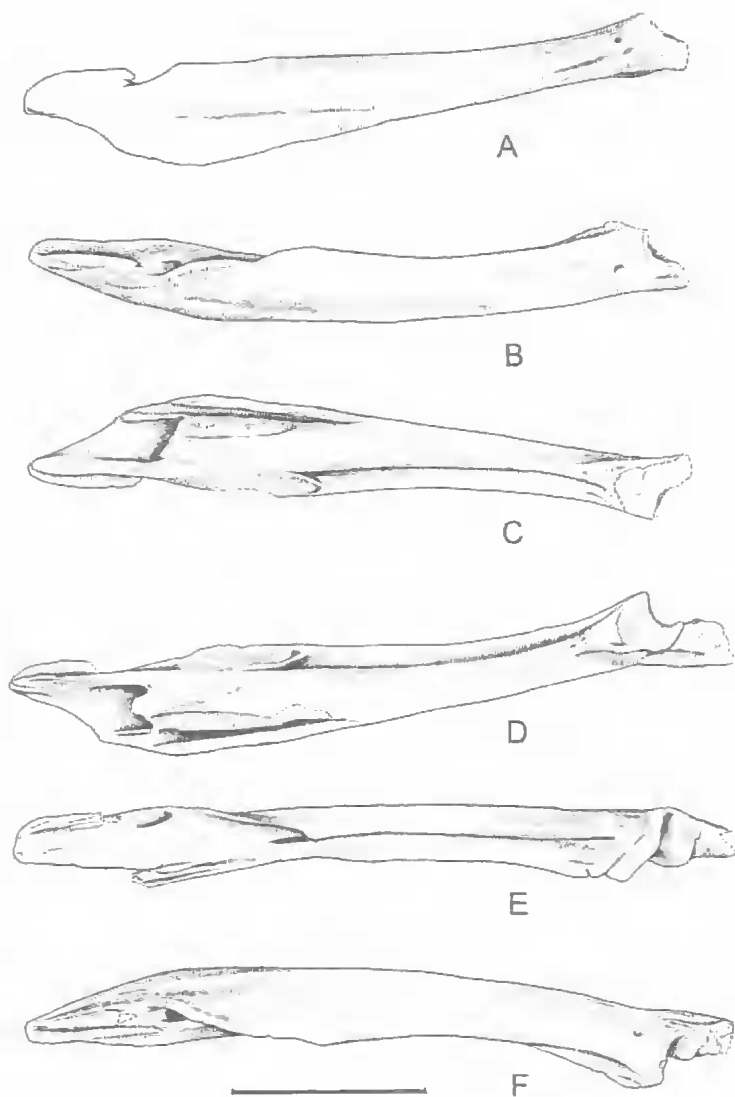


FIG. 4. *Nanowana godthelpi* sp. nov., QMF31383, 31384, paratypes. compound lower jaw bones, CS Site. A-C, left compound in lateral, dorsolateral, and medial views (note missing articular). D-F, right compound in medial, dorsal, and dorsolateral views. Scale=5mm.

edge expanded anterodorsally, for anterior 1/3 of length anterior to the coronoid process. Surangular foramen, opening anteriorly, not exposed laterally or medially, in a shallow dorsal trough between lowest point of surangular lamina and edge of coronoid facet. Facets for coronoid and angular meeting at a very small angle below this point; their line of contact nearly horizontal, only

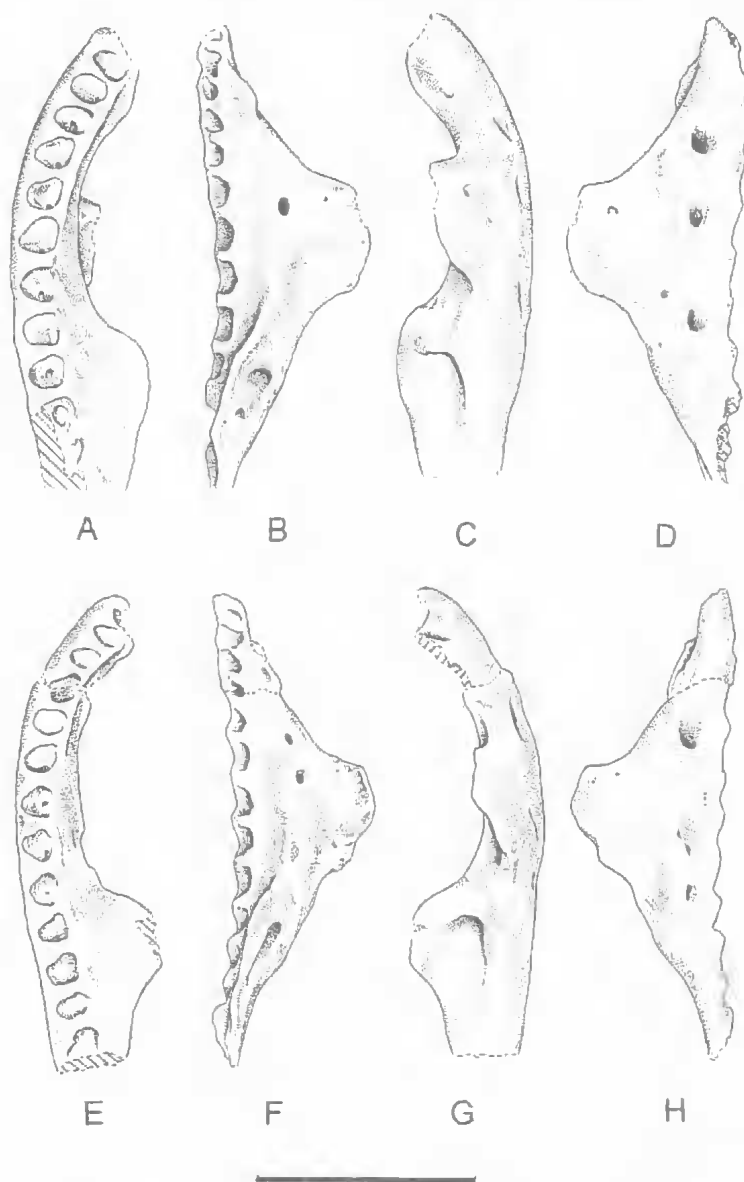


FIG. 5. *Nanowana godthelpi* sp. nov., paratype, maxillae, CS Site, A-D, QMF31386, in ventral, medial, dorsal, and lateral views. E-H, QMF31380, in ventral, medial, dorsal, and lateral views. Scale=5mm.

a short section preserved on either side. In lateral view the anterior edge of the compound rounded dorsally, separated by a right angle from a deeper ventral concavity. In medial view, a long, tapering notch enclosed in the facet for the angular, nearly reaching its posterior end (just posterior to middle of length of compound). A medial anterior process (defined by dorsal and ventral longitudinal fissures) bearing the continuation of facets for the coronoid and angular, and probably also con-

tacting the splenial and dentary, broken on both sides. Left compound similar to the right, but broken posteriorly through the articular facet.

When placed in articulation, the right compound and dentary forming a smoothly curved structure, with total straightline length approximately 29.5mm.

Other paratypes and referred jaw elements (partial dentaries, maxillae, palatines, pterygoids) show some individual variation (Figs 5, 6) and probably ontogenetic changes of proportions (allometry): the smallest dentary, QMF 23056, is relatively deeper than larger specimens (Table 1), while the largest, QMF23076, is relatively slender except for a particularly deep upper posterior process.

Vertebrae. In shape and proportions, vertebrae similar to, and intermediate between *Yurlunggur* and *Patagoniophis* and differ conspicuously from *Alamitophis*, *Wonambi* and *Madisoia*. Typical anterior, middle and posterior trunk vertebrae recognised (cf. LaDuke, 1991, Scanlon, 1992, 1993); most anterior vertebra possibly 3rd cervical (cf. *Y. camfieldensis* Scanlon, 1992, fig. 1A). Centrum in ventral view relatively long, similar in proportions to *Patagoniophis* sp. but with the sub-

central ridges nearly straight rather than strongly concave. Cotyle slightly wider than the zygosphene, which is wider than the neural canal (all about equal in the most anterior vertebra); condyle and cotyle wider than deep, ventral margins flattened in anterior and middle trunk, rounder posteriorly.

Zygapophyseal facets inclined at about 20° from the horizontal (at mid-trunk; flatter anteri-

only, slightly steeper posteriorly), defining planes passing through the internal lateral ridges of the neural canal and intersecting just above its base. Facets broader and more angular in outline (especially the prezygapophyses) in the largest midtrunk vertebrae, with long axes inclined at about 45° from the sagittal plane (somewhat more longitudinal in most anterior and posterior elements). Prezygapophyseal accessory processes lacking, outer face of the prezygapophysis with a buttress-like ridge extending anterolaterally to or slightly beyond the edge of the facet.

Zygosphenes shallower than the neural canal, with facets defining planes intersecting below the floor of the canal; dorsal edge in anterior view flat, slightly arched or arcuate; below it are shallow concavities defining a dorsal ridge and lateral lobes, with sharp ridge separating the anterior face of the zygosphenes from the internal roof of the neural canal. In dorsal view the anteriorly convex dorsal ridge and lateral lobes distinct in mid-trunk vertebrae, but in the most anterior and posterior elements median prominence less developed and zygosphenes broadly concave.

Paradiapophyses similar to *Yurlunggur* or *Patagoniophis*, extending laterally beyond the zygapophyses only in the most anterior and most posterior vertebrae.

Roof of zyganchrum horizontal, either uniform in depth or thickening laterally, demarcated from the concave lateral parts of the neural arch by angular 'shoulders', with concavity directed more dorsally than laterally in the most posterior vertebrae because of the shallower neural arch and steeper postzygapophyses.

One or two small paracotylar foramina on either side of the cotyle, usually 2 lateral foramina on either side posterior to the diapophyses. Sub-

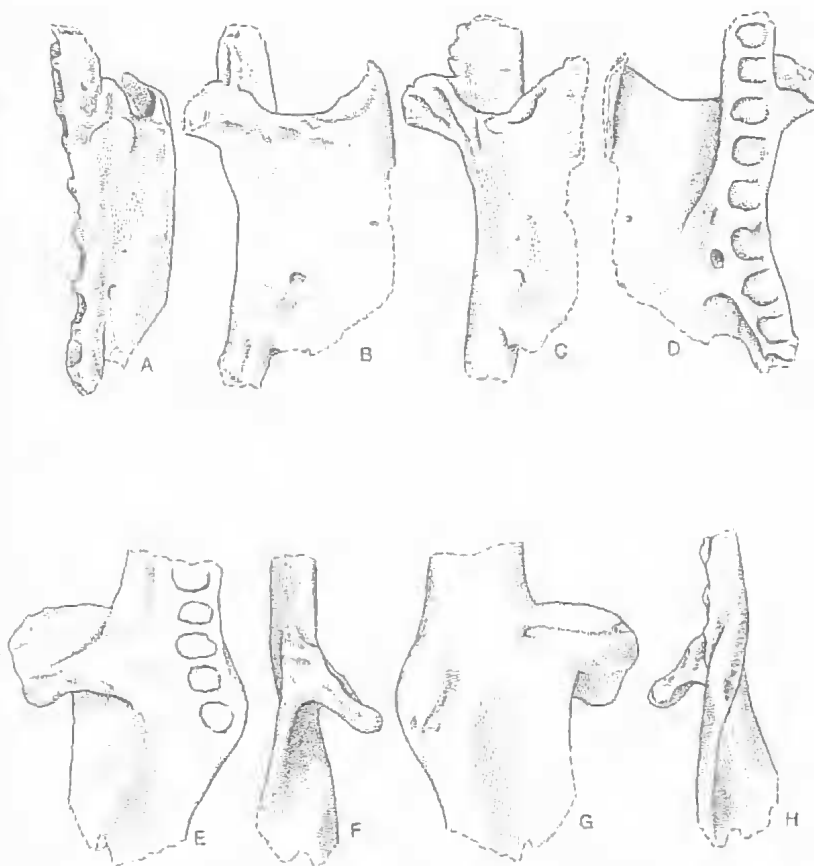


FIG. 6. *Nanowana godthelpi* sp. nov., referred elements from Upper Site possibly from a single individual. A-D, left palatine, QMF23066 in lateral, dorsal, dorsomedial, and ventral views. E-H, right pterygoid, QMF23067, in ventral, lateral, dorsal and medial views. Scale=5mm.

central foramina usually single on each side, small. Parazygantral and zygantral foramina larger, usually single on each side, frequently in distinct fossae. Some vertebrae with small foramina on the anterior face of the prezygapophysis below the facet.

Ventral face of centrum concave between the haemal keel and subcentral ridges. In the anterior trunk hypapophysis projecting well below centrum from its posterior half, with either an angular or sinuous anteroventral edge, and near-vertical posterior edge; in more posterior vertebrae the keel weakly sinuous to nearly straight in lateral profile. Haemal keel with median, keel-like hypapophysis reducing in depth from the cervical to mid-trunk regions; lateral ridges on the keel (initially just posterior to the subcentral foram-

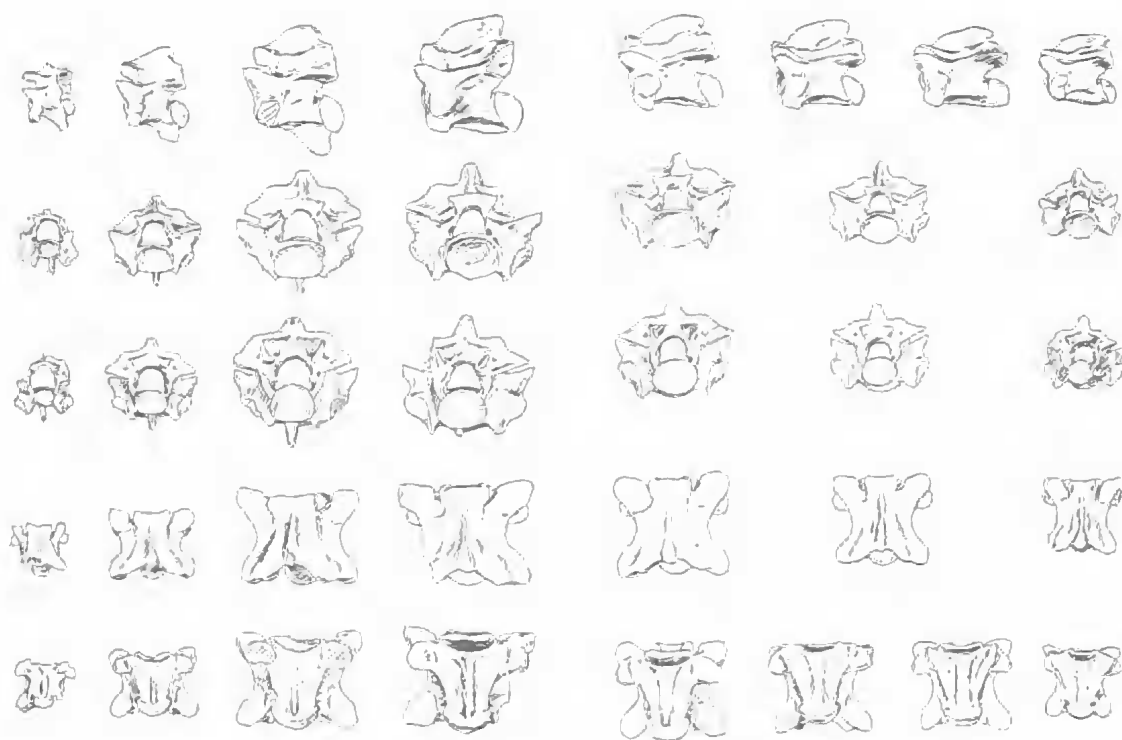


FIG. 7. *Nanowana godthelpi* sp. nov., QMF19741, series of vertebrae from CS Site, possibly from the same individual as the holotype (QMF31379).

ina) from the approximate location of the largest vertebrae in the skeleton, ridges increasing in size in more posterior vertebrae and posterior point of the median keel fading away, leaving the ridges as paired hypapophyses, ventrolateral swellings of the keel. Haemal keel defined by smooth depressions in the anterior trunk, these becoming better defined more posteriorly and approaching the cotylar rim. More posterior vertebrae with distinct channels between keel and subcentral ridges (subcentral paramedian lymphatic fossae, LaDuke, 1991).

Most vertebrae from all regions of the body with swellings on the neural arch roof on either side of the spine, forming short longitudinal ridges. Similar features in some *Wonambi* from Riversleigh are associated with small foramina (not the case here). Vertebrae similar to these and referred to *Nanowana* sp. (most of them probably *N. godthelpi*) from numerous sites at Riversleigh, including well-preserved examples from Wayne's Wok, Wayne's Wok 2, Mike's Menagerie, and Upper Site.

Vertebrae of the cloacal region (Fig. 8) proba-

bly from a single individual with short centrum, broad zygosphenes, and condyle smaller than neural canal (regional features allowing increased flexibility in this region). Haemal keel smooth (lacking the median ridge of *Wonambi* spp.), not or barely projecting below the centrum posteriorly. Two largest vertebrae with paradiapophyses indicating articulated ribs, but on one side of one of them the articular surface is expanded and roughened suggesting an immobile cartilaginous attachment (i.e. transitional to fixed lymphapophyses). Three others with lymphapophyses (broken distally); another with stumps of cylindrical fixed ribs, possibly forking more distally.

***Nanowana schrenki* sp. nov.**
(Figs 9-12, Table 2)

MATERIAL. Holotype QMF31395, a right palatine from early Miocene Upper Site, Godthelp Hill. Other Material: Upper Site: Maxilla fragments QMF 31390, 31391, 31394. Mike's Menagerie Site: Dentary QMF31392 and vertebra QMF23043. Camel Sputum Site: Dentary QMF23051; maxilla fragments QMF23082, 31388.

TABLE 2. Measurements of ETYMOLOGY. For *Nanowana schrenki* sp. nov., Friedemann Schrenk, holotype and referred jaw elements. Abbreviations as in Table 1, with addition of dd8 = depth of dentary at 8th alveolus.

QMF	31395	31394	23082
IND.	U1	U	M
ptl	4.7	-	-
pci	2.5	-	-
pli	3.8	-	-
ptw	2.5	-	-
pcw	1.3	-	-
prw	0.6	-	-
pmw	0.6	-	-
mpw	-	1.7	-
mph	-	2.0	(1.0)
Dentaries			
QMF	23051	31392	
Ind.	C1	MM	
mff	3	3	
d1	(16.7)	(7.1)	
d1.5	13.7		
d1.7	15.6		
d1f	12.6		
d4r	-	5.3	
d4.5	9.3	4.1	
d4.7	11.2	4.6	
d4f	8.3	3.5	
d1.7	6.7	-	
dd8	2.3	1.0	
dpp	0.7	0.4	

view. Three mental foramina, the third posterior to the 7th tooth.

DESCRIPTION. Holotype. Alveoli 11, teeth ankylosed in 1, 3, 4, 5, 6, 8, 9, 10, 11; only 8, 10 and 11 complete. Teeth with a simple curve, directed posteriorly. Tooth row deflected slightly medially anteriorly, laterally posteriorly. Maxillary process slightly wider than the tooth-bearing bar, extending from between 2nd and 3rd to between 6th and 7th teeth, with an anteriorly sharp lateral notch, and sharp posterolateral angle. Ventral surface of the process with a diagonal ridge from the rear of the 4th tooth to the posterolateral angle, defining an anterolaterally concave facet to articulate with the palatal process of the maxilla. Anteriorly, the edge of the lateral process

continuous with a dorsolateral ridge extending to the anterior tip of the tooth-bearing process. A second ridge diverging medially from the anterolateral corner of the process, bearing a distinct knob above the tooth row and continuing onto the anterior edge of the choanal process, level with the rear of the 4th alveolus. Anteromedial corner of choanal process (to articulate with posterior process of vomer and possibly parasphenoid) missing. Medial edge intact, and smoothly convex, from level of 7th alveolus to rear of tooth row, but posterior process broken off. Cusp defining lateral edge of choanal trough diverging posteromedially from the 6th tooth, disappearing level with the 8th; 2 foramina close together in the space between and medial to 7th and 8th alveoli, one of them piercing the choanal plate to emerge dorsally in a more medial position and opening medially. Tooth-bearing bar pointed posteriorly, tapering from the 9th tooth, a broad parabolic surface for the retractor pterygoidei on the ventral face with its apex beside the 9th, becoming less distinct posterolaterally. Deep notch to articulate with the pterygoid on the dorsal side between the tooth row and posterior process, extending to above the anterior edge of the 10th tooth. Distinct growth lines through the translucent choanal plate parallel to its curved medial edge.

DIAGNOSIS. Lateral process of palatine about as long as 4 alveoli (3-6), with dorsolateral margin strongly notched; ventral ridge of palatine maxillary process without distinct angular concavity, matching smooth edge of maxillary palatine process. Maxilla estimated to have about 19 tooth positions; palatine with 11, pterygoid unknown, dentary 18 (or 17-18). Teeth ankylosed normally; 2nd to 4th of dentary, and 4th to 7th or 8th of maxilla, much larger than others. Dentary tooth row nearly straight in dorsal

view. Three mental foramina, the third posterior to the 7th tooth.

REFERRED MATERIAL. Maxilla represented by several fragmentary specimens from different sized individuals (Fig. 10). Tooth row curves medially anteriorly (QMF23082), with a strong gradient of increasing alveolar diameter from 1 to 5; 5 and 6 subequal. Dorsal edge is a sharp, concave dorsomedial crest, extending to a high dorsal process, levelling off above 6th alveolus; this crest divides anteriorly, enclosing a shallow trough above the first two alveoli (thus, maxilla partially flooring nasal cavity). Lateral face mostly convex, with a shallow longitudinal trough including a large foramen (opening anterior and ventrad) above rear of the 4th tooth; a smaller foramen near the dorsal edge above the 5th. Medial face concave, with a trough just below the dorsomedial ridge containing a small foramen just anterior to the medial one. Middle part of maxilla (QMF31394) with distinct knob-like posterior part of prefrontal process and sloping suborbital portion, becoming more rod-like and wider than high posteriorly. Tooth size decreasing sharply, with increased alveolar spacing, just behind prefrontal process; longest (7th or 8th?) 2.2mm long, curved at middle but straight

distally, with medial and lateral cutting ridges (like longest tooth of dentary QMF31392, see below); more posterior teeth (broken before drawing) with simple curve, about half as long. Palatine process diverging from tooth row at last large tooth and reaching maximum width between the next 2 alveoli. Medial edge of the palatine process quite smooth, matching the concavity of the maxillary process in the holotype; large opening on dorsal face of process for palatine nerve and blood supply through several foramina on lateral surface. Teeth on posterior part of maxilla (QMF31391) still reducing in size from anterior to posterior, and with slight double curve. Posterior part triangular in section, with near vertical lateral and oblique dorsomedial faces both slightly concave, meeting at a dorsolateral ridge. Lateral edge straight, medial edge produced as ridge with convexity probably marking anterior limit of ectopterygoid.

Dentaries. Two right dentaries, differing considerably in size (Fig. 11), represent the lower jaw in this species. QMF31392 with complete row of 18 alveoli, teeth ankylosed in 1 (possibly), 3, 6, 8, 10, 11, 13, 15, 16, and 18; 10th broken, other teeth in tact, and a replacement tooth apparently *in situ* behind 15th. QMF23051 has 17 alveoli, but another may have been present posteriorly; 1, 4, 5, 6, 7, 9, 11, 12, 13, 14 and 15 ankylosed, but all teeth broken near base (the jaw has also been broken through 3rd alveolus and subsequently healed in life). 1st alveolus approximately same size as 5th, but 2nd to 4th considerably enlarged; 3rd nearly twice diameter of 5th, size decreasing gradually more posteriorly; in the small specimen, lengths of teeth from anterior edge of base to tip (mm) -, -, 1.26, -, -, 0.61, -, -, 0.63, -, -, 0.55, -, 0.52, -, 0.40, -, 0.37, 0.28. Anterior alveoli (1-3) deflected ventrad and mediad relative to rest of tooth row, which is moderately concave dorsad

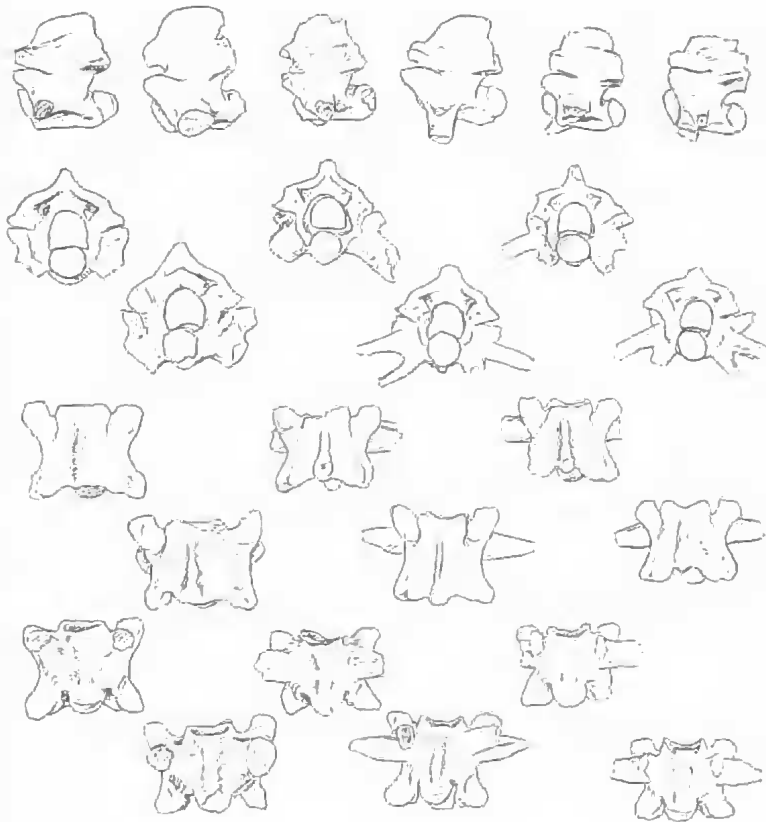


FIG. 8. *Nanowana godthelpi* sp. nov., series of most posterior trunk and cloacal vertebrae from Upper Site, possibly from the same individual as jaw elements in Fig. 6. Lateral, posterior, dorsal, and ventral views.

but only very weakly concave mediad. Third tooth directed slightly laterad as well as posteriad; other teeth mediad, more strongly towards the rear of the tooth row. Each tooth with a weak lateral and medial cutting edge near the tip. Dentary deepens gradually from anterior to posterior. Three mental foramina open anteriorly below alveoli 4, 7 and 9 (QMF31392) or 3, 6-7 and 8 (QMF23051), decreasing in size posteriorly. A shallow dorsal trough medial to 3rd and 4th alveoli defined by a dorsomedial crest. Lateral fossa extends as far anteriorly as the rear of the 13th tooth, blunt in outline; posterior edge of the vertical intramandibular septum smoothly concave, extending forward to between the 14th and 15th teeth. Differences between the two include shape of Meckel's groove (tapering more strongly in the small jaw, dorsal edge composed of two sharply defined sections separated by a short gap below 8th-9th alveoli, but no gap in the larger speci-

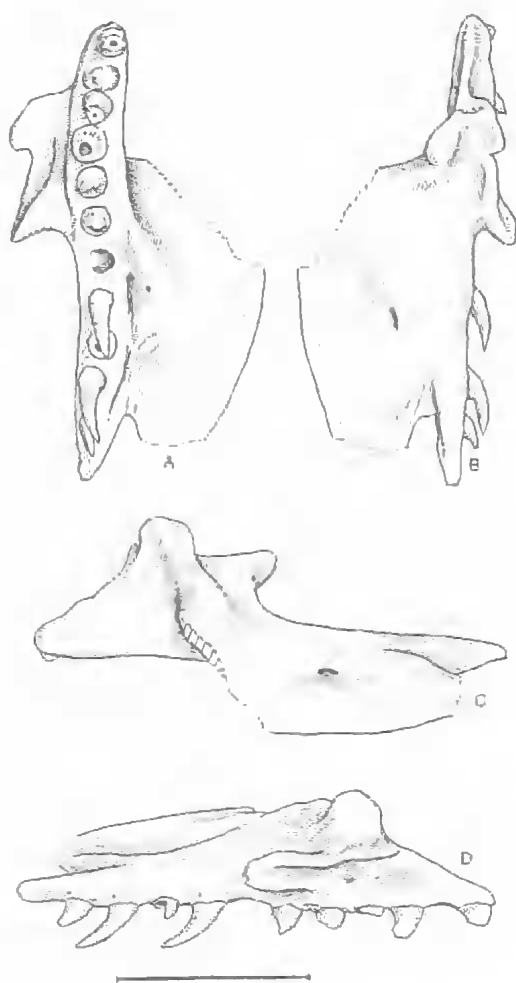


FIG. 9. *Nanowana schrenki* sp. nov., holotype, QMF31395 from Upper Site, palatine in ventral (A), dorsal (slightly lateral) (B), dorsomedial (C), and lateral (D) views. Scale bar=2mm.

men), upper facet for splenial (with posteromedial angle in the smaller, but a free-ending process in the larger), and lateral fossa (constricted in the smaller by deepened upper posterior process); both narrowest in the region of the 6th to 8th alveoli; but the larger specimen is relatively broader posteriorly.

Vertebra (Fig. 12) from mid-trunk of a juvenile, with short broad centrum, large neural canal, and condyle and cotyle much wider than deep. Weakly defined subcentral ridges narrow only slightly behind the parapophyses, posterior half of centrum nearly parallel-sided except for a shal-

low, short precondylar constriction. Blunt haemal keel extending from just behind the cotylar rim, posteriorly forming a slightly prominent single hypapophysis extending below the condyle. Keel defined laterally by broad shallow depressions. Comparisons with *Yurlunggur* or *Patagoniophis* would imply that a haemal keel of this form indicates a vertebra from close to the cardiac region (transitional between prominent single hypapophysis anteriorly and flattened or double keel posteriorly), and would thus be among the largest in the skeleton. Condyle and cotyle about twice as wide as deep, slightly oblique in lateral view; cotyle wider than the neural canal but not as wide as the zygosphenes. Zygapophyseal facets inclined at less than 20° above the horizontal, defining planes which intersect near the middle of the neural canal. Prezygapophyseal facets obovate, with transverse anterior edge; postzygapophyseal facets more smoothly oval, and somewhat prominent posteriorly in dorsal view. Both pairs of facets arc elongate anteroposteriorly, with long axes at about 35° to the sagittal plane (as in anterior, but not middle trunk vertebra of *Patagoniophis* sp. cf. *P. parvus*; Scanlon, 1993). No prezygapophyseal processes.

Paradiapophyses directed ventrolaterad, slightly wider than prezygapophyses, not extending ventral to cotylar rim. Interzygapophyseal ridge smoothly concave laterally, only slightly wider than the centrum, and weakly defined in lateral view.

Zygosphenes thin, slightly arched; anterior edge smoothly but weakly concave (again, like anterior rather than middle vertebrae of *Patagoniophis*). Zygosphenal facet (preserved on left only) dorsoventrally shallow, with dorsally convex upper and lower edges, inclined at about 45° from vertical; a plane tangent to the facet would pass close to the centre of the neural canal.

Neural canal arched, about as high as wide, lacking internal lateral ridges. Neural arch low, with shallow concavities above and below the level of the zygosphenes and extending to the posterior edge. Zygantral roof arched, thickness uniform across its width. In dorsal view, rear of neural arch forming a broad concavity above the zygantrum, interrupted by the neural spine. Low neural spine formed by a narrow, but sharply defined anterior lamina rising from the rear of the zygosphenes and applied to a higher, columnar portion posteriorly, overhanging the zygantrum. Dorsal surface of column broken off, with a sinus visible within the neural arch. Lateral and sub-

central foramina present, any other obscured by dendrites.

TROPHIC SPECIALISATIONS OF NANOWANA

N. godthelpi sp. nov. The homogeneity in size, morphology and approximate stratigraphic position of these toothless but otherwise well-preserved jaws makes it appear probable that the lack of ankylosed teeth is a natural (and apomorphic) characteristic. To quote Owen's (1840) conclusion on the 'dislocated' tail of ichthyosaurs, the toothless condition '... is too uniform and common to be due entirely to an accidental and extrinsic cause'. Variation in the shape and size of alveoli along the tooth rows, and the presence of 'frothy' bone similar to bone of attachment in some cases, indicates that different stages of replacement are represented, so that absence of teeth is not explained by synchronised replacement. Some of these specimens are practically intact, preserving delicate processes, and not worn in such a way as to account for the absence of even stumps of teeth; in most other specimens from the same deposits, parts of teeth are typically retained even after heavy wear. The alveoli are shallow, rather rectangular pits, so that a thecodont type of implantation is not indicated as an alternative to ankylosis.

Failure of teeth to ankylose at any stage is rare among squamates, first reported by Savitzky (1981). *Anomochilus weberi*, a small fossorial 'anilioid' (Anomochilidae is possibly the sister taxon to other

living Alethinophidia; Cundall et al. 1993), apparently has fibrous tooth attachment rather than ankylosis (Cundall & Rossman, 1993). There are also several lineages of snakes, and one genus of

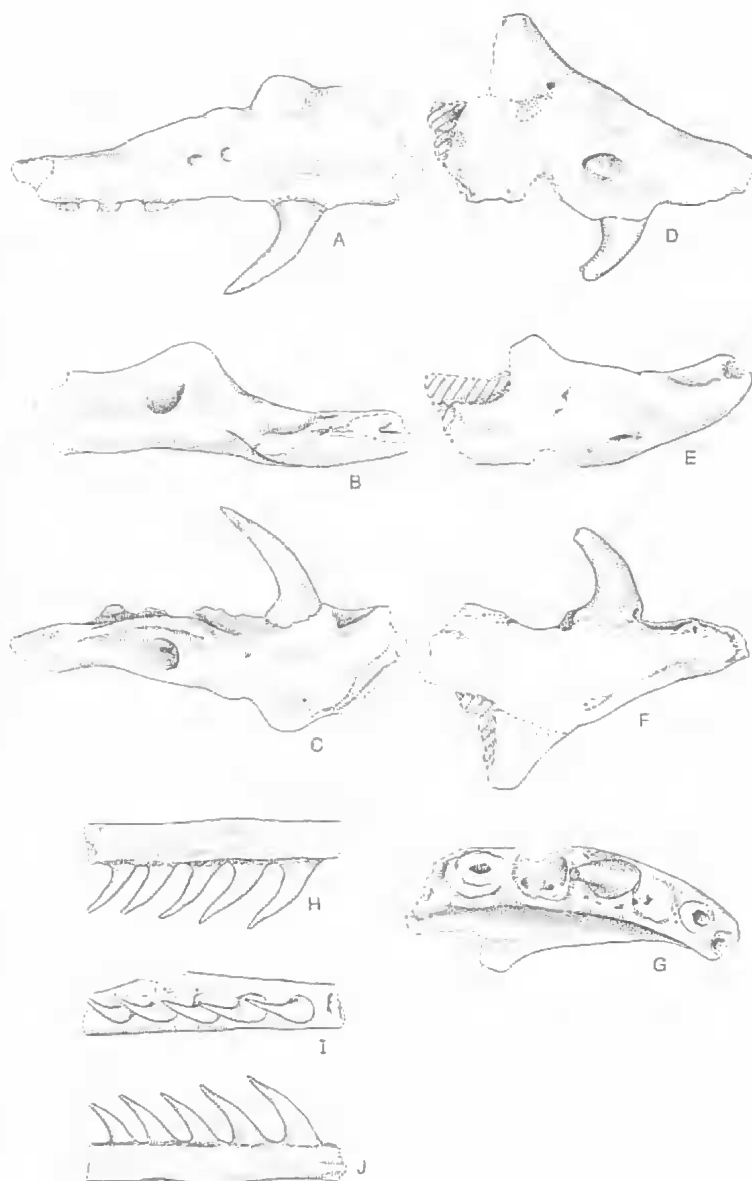


FIG. 10. *Nanowana schrenki* sp. nov., maxillary fragments. A-C, QMF31394, Upper Site, middle part of right maxilla in lateral, dorsal, and medial views. D-G, QMF23082, CS Site, anterior right maxilla in lateral, dorsal, medial, and ventral view. H-J, QMF31391, Upper Site, posterior left maxilla in medial, ventral, and lateral views. Not to same scale.

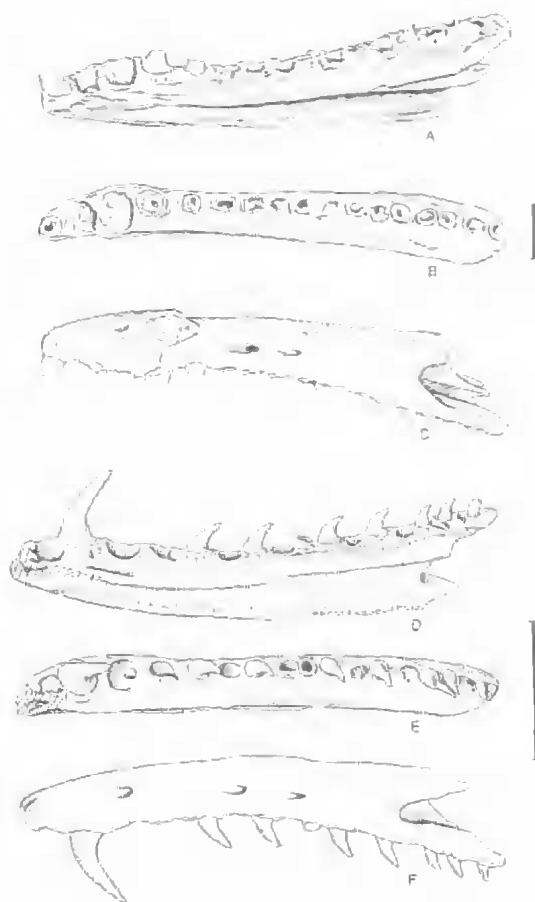


FIG. 11. *Nanowana schrenki* sp. nov., right dentaries. A-C, QMF23051, CS Site, in medial, dorsal, and lateral views. D-F, QMF31392, MM Site, in medial, dorsal, and lateral views. Scale bars=2 mm.

lizards, where the attachment is not only fibrous but forms a functional hinge allowing each tooth to fold posteriorly under pressure and return upright when released (Savitzky, 1981, 1983; Patchell & Shine 1986c; cf. Edmund, 1969:141). This hinge mechanism has been interpreted in each case as an adaptation to feeding on scincid or gerrhosaurid lizards in which the scales are underlain by osteoderms; the hinged teeth are

thought to act as a ratchet mechanism, folding back rather than penetrating the dermal armour, and locking in an upright position against the edges of the scales when the prey is oriented head-first for swallowing. In extant snakes other functionally associated apomorphies also occur; the teeth are small and numerous, often with a spatulate rather than conical tip, and lack enamel on the posterior surface; and the levator anguli oris muscle (inserting on a long upper posterior process of the dentary) is enlarged (Savitzky, 1981). In the pygopodid *Lialis* teeth are of similar form, and instead of increased intramandibular kinesis there is pronounced kinetic ability at the frontoparietal joint (mesokinesis; Patchell & Shine 1986b). Both types of kinesis allow the jaws more effectively to surround and compress a cylindrical prey item, immobilising or even asphyxiating it. An equivalent adaptation for prey-holding (without hinged teeth) is seen in the largely scincivorous holyeriid snakes, in which the required kinesis is provided by the uniquely derived intramaxillary joint (Cundall & Irish, 1989).

Savitzky (1983) described this set of adaptations to feeding on skinks, which has evolved independently in several lineages, as an instance of a 'coadapted character complex', among other cases of 'durophagy' (feeding on hard-bodied prey). Other durophagous snakes have distinct specialisations, and feed on other kinds of 'hard' prey such as snails (pareine and dipsadine colubrids) or crabs (the homalopsine *Fordonia*). 'Durophagy' is thus a broad concept. I introduce 'arthrodonty' to refer specifically to the 'hinge-toothed' mode of durophagy.

While soft-tissue structures such as fibrous hinges cannot be observed in fossils, absence of ankylosis implies that attachment was fibrous and potentially flexible. *N. godthelpi* jaw material is similar to that of extant arthrodont species after maceration, especially *Xenopeltis* (Savitzky, pers. comm.). Hutchinson (1992) demonstrated that scincid lizards were abundant and diverse in the Tertiary at Riversleigh; skinks today represent a major food source for small terrestrial predators, including most extant Australian snake species (Shine, 1991). As functional arthrodonty has evolved in several lineages in association with predation on skinks, its presence in *N. godthelpi* is a plausible explanation for the lack of ankylosis.

N. godthelpi appears to be less specialised than each of the extant arthrodont snake lineages in some respects. The high number of nearly uni-

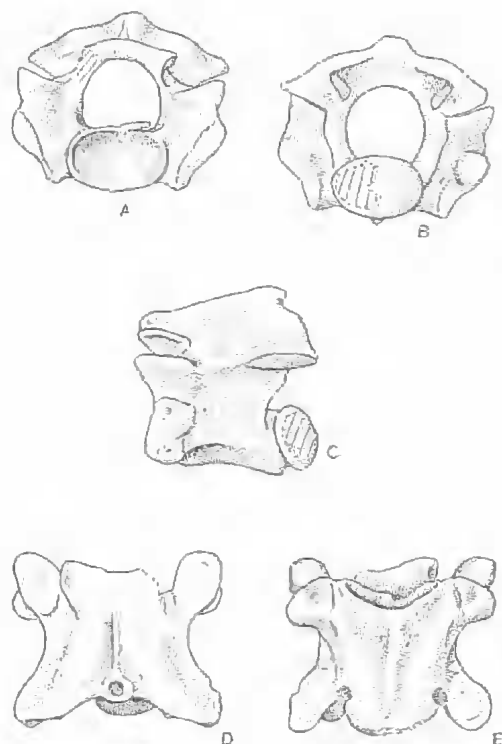


FIG. 12. *Nanowana schrenki* sp. nov., vertebrae, QMF23043, MM Site, probably same juvenile as dentary QMF31392 (Fig. 11) in anterior (A), posterior (B), lateral (C), dorsal (D) and ventral (E) views.

form maxillary alveoli is typical of an arthrodont species, but a similarly long tooth row is present in *Wonambi naracoortensis* (Barrie 1990), and is therefore likely to be a retained ancestral condition rather than a specialisation. The overlap between dentary and compound is moderate, without any great elongation of the tooth-bearing posterior process; the extreme condition in extant arthrodont lineages may be precluded by the probable insertion of *m. levator angulioris* on the relatively large coronoid rather than the dentary, but the overlap is actually shorter in this species than in *Wonambi*.

The dentary alveoli of *N. godthelpi* are considerably larger, especially in the middle part of the row, than those of the maxilla, so the lower teeth may have functioned differently, and possibly lacked a functional hinge. In *Xenopeltis*, relatively large teeth are present on the middle part of the palate (posterior palatine and anterior pterygoid), but these appear to be fully hinged. While fibrous attachment of 'sessile' teeth has been

reported only in one highly unusual extant taxon, *Anomochilus*, it is possibly a necessary precursor or incipient stage of arthrodonty (see below), and a mixed or 'semi-arthrodont' condition in *N. godthelpi* seems possible.

Nanowana schrenki sp. nov. In the absence of articulated or strongly associated material, referral of jaw elements described here to a single taxon can only be provisional. In particular, the 2 near-complete dentaries differ in several respects which make their assignment to the same species doubtful: in QMF23051 the upper edge of the Meckelian groove is a continuous ridge and extends posteriorly as a free-ending process, while in QMF31392 it is interrupted at the 9th alveolus, and appears to end abruptly. (Additionally, the larger specimen broadens more posteriorly, while the small one is widest at the 3rd tooth, but this difference may be allometric.)

The teeth of snakes play several roles in the capture, subdual, puncturing or laceration, and swallowing of prey; in general they will be adapted for a combination of functions, but often either a single function is dominant, or certain stages are either not required (e.g. because inactive or defenceless prey is taken) or carried out extra-orally (e.g. constriction). Teeth specialised for different functions are often separated between the front and rear of the mouth, in some cases with diastemata between teeth of different morphology (Frazzetta, 1966; Scanlon & Shine, 1988; Cundall & Irish, 1989).

Numerous terms have been introduced for different patterns of tooth size and fang location (Smith 1952). Primitive snakes (*Dinilysia*, anilioids) are isodont or mesodont, with relatively few, stout teeth; while also capable of constriction, they use a powerful 'crushing' bite in subduing prey (Frazzetta, 1970; Greene, 1983). Such a 'crushing' method seems possible for *Madtsoidia* cf. *M. bai*, in which the dentary is heavily built and bears relatively few teeth (Hoffstetter, 1960), but not for Australian madtsoiids. Different patterns of tooth-size variation in upper and lower jaws are known in each of the 4 best-represented taxa:

In *Wonambi naracoortensis* the very numerous teeth (25 in the dentary, 22 or 23 in the maxilla) are proterodont, sharp and strongly inclined posteriorly and medially (Barrie, 1990); the jaws are shallow, suggesting a limited role in subduing prey, and more emphasis on holding and swallowing functions. This implies that an extra-oral method of subduing prey (probably constriction) was well-developed. When the upper and lower

jaws are both proterodont, teeth often have a sigmoid curvature with the tips directed somewhat anteriorly as in many pythons (Frazzetta, 1966), and seems to be associated with relatively soft-bodied prey such as mammals, birds, earthworms (McDowell, 1969) and eels (Smith, 1926; Cogger et al., 1987).

Nanowana godthelpi apparently had a nearly isodont marginal dentition. No complete tooth crowns have been reported for this species, but based on alveolar sizes it was weakly proterodont on the maxilla and mesodont on the dentary (Figs 1, 3).

The condition in *Yurlunggur* is less clear but apparently the opposite; a dentary with well-preserved teeth (Archer et al., 1991:71) is proterodont, while the maxilla was apparently mesodont (Scanlon, 1996).

N. schrenki can be described as megadont (Smith, 1952), having regions of distinctly enlarged teeth. Otherwise it has the same pattern of enlargement as *Yurlunggur*, opposite to that of *N. godthelpi*, being mesomegadont on the maxilla and promegadont on the dentary. The dentary is relatively longer and less robust than in *Madtsoia* or *Dinilysia*, but not depressed as in *Wonambi*; the teeth are intermediate in number and in morphology (stouter and more erect than *Wonambi*, but not so much as in *Dinilysia* or anilioids); and the enlarged teeth are a uniquely derived condition within Madtsoiidae (albeit convergent with many other lineages of snakes).

Many snakes share this pattern of enlarged teeth at the front of the dentary and the part of the maxilla below the prefrontal articulation, whether or not they are set off by diastemata or local minima of tooth size. On the basis of occurrence in scincivorous colubroids such as *Lycodon*, *Glyphodon*, *Demansia*, and *Hemiaspis signata* (but not the anurophagous *H. dameli*; Boulenger, 1896; Worrell, 1961; Shine, 1991; Cundall & Irish, 1989; pers. obs.), this is here tentatively considered an adaptation to hard-bodied prey, often skinks. Snakes with enlarged teeth offset between upper and lower jaws are able to trap hard, cylindrical prey items between a notch in one tooth-row and one or more enlarged fang-like teeth (sometimes true fangs) in the other (Cundall & Irish, 1989). As well as this 'trapping' function, having only a few long teeth in each jaw maximises the probability of hard-bodied prey being deeply punctured, whereas this is avoided in arthrodont forms.

EVOLUTION OF TEETH AND ATTACHMENT

Snake teeth are slender compared to other vertebrates; they break frequently during normal use and are quickly replaced (Edmund, 1969). They have reduced occlusal area (sacrificing strength) to increase sharpness and depth of penetration. Tooth form is a compromise between competing selective forces defining a 'fitness landscape' over attainable phenotypes (Wright, 1932), and local optima will be attained only if intermediate states are evolutionarily stable. If the rate of breakage is too high, prey capture or swallowing efficiency (and consequently fitness) will be low.

During the stages of feeding on a given range of prey types with given neuromuscular repertoires, forces on the tooth come from particular directions with greater or lesser frequency and magnitude, so it will generally be favourable for the tooth to be asymmetrical rather than a simple cone. The orientation of 'cutting ridges' (which function as buttresses as well as blades), curves in the shaft, and the shape of the tooth base, will confer maxima of resistance in one or more directions, at the expense of minima elsewhere.

Horizontal components of pressure (shear stress) at the tip of an approximately conical tooth are converted to bending stresses at the base, i.e. compression at one side and tension at the other. The magnitudes of these forces will depend on base diameter, but only tension and shear will tend to either break the shaft or disrupt the attachment of tooth to bone. Bone of attachment can apparently withstand such stresses within a wide range of values of the ratio of tooth length to basal diameter. A fibrous connection will remain stable at low values of this ratio (short, broad teeth as in *Anomochilus*), and at intermediate values will have enough elasticity to return the tooth upright after displacement (functional arthrodont condition). At high values (longer, slender teeth) a fibrous attachment would merely bend passively, without developing enough tension to right the tooth; the orientation of the teeth would then not be precisely controllable, and during prey capture and ingestion they would more often encounter shear stresses at unfavourable angles, leading to rupture. Such a condition (elongate, slender teeth with fibrous attachment) is unknown in any living snakes, and would presumably be evolutionarily unstable for most diets and feeding methods.

This consideration of the forces applied at the tooth tip and base suggests that arthrodonty and elongate teeth are mutually exclusive conditions.

Thus the specialisations of dentition and jaw morphology in *Nanowana* are most likely to be independently derived from the nearly isodont, ankylosed condition of other madtsonids, and apparently represent alternative solutions to the problem of feeding on hard-scaled lizards.

Healed breaks of the jaw elements (particularly dentaries) are not uncommon in snakes (pers. obs.), and presumably result in most cases from attempts to capture or subdue relatively large and powerful prey. Sublethal trauma associated with particular morphological specialisations may be an indicator of mechanisms of selection; there are upper limits to prey size and strength for every species of predator, and both prey selection and behavioural aspects of prey-handling, as well as morphology, will be subject to selection. The break through the third dentary alveolus of QMF23051 (*N. schrenki* sp. nov.) would have occurred most easily (i.e. greatest stress would occur) while the 3rd alveolus was unoccupied, and while a prey item was held by the enlarged 2nd tooth, but not the smaller posterior teeth. Fractures of this kind could be expected to be less common (all else being equal) with a more uniform dentition, but this possible disadvantage of megadonty may have been outweighed by an increased rate of capture success, or of retention once a prey item was secured behind (or impaled on) the enlarged dentary teeth.

The ribbon-like posterior maxilla of *N. godthelpi* presents an even more fragile appearance, but no specimens suggest breaks during life. While this is negative evidence, the rarity of such breaks would tend to support the presence of a jugal in the suborbital region. Presence of a jugal in *Wonambi naracoortensis* can similarly be inferred from the oblique trough crossing the maxilla (Barrie, 1990; Scanlon, 1996) which would otherwise be an obvious point of fragility.

SYMPATRY OF RELATED SPECIES WITH SIMILAR DIETS

The two species of *Nanowana* occur together in at least 3 Sites, existing sympatrically for a significant period. They are thought to have had similar diets (skinks), and similar adult size. They thus occupied quite similar niches, and were strictly equivalent ecologically. They may have differed in aspects of behaviour which would not be discernible in the fossil record, but at least a difference in habitat can be suggested.

The different representation of the two species when found together (minimum number of indi-

viduals, number of identifiable elements, and quality of preservation) implies that *N. godthelpi* was more abundant close to the sites of deposition, whereas *N. schrenki* may have been less abundant locally, and the more damaged remains transported from further afield (cf. LaDuke, 1991). Thus *N. godthelpi* lived near water (possibly riparian, probably closed forest), whereas *N. schrenki* may have lived further from water, possibly in more open or drier areas such as clearings or rocky hills.

Most sites where *Nanowana* vertebrae have been found have not produced jaw elements diagnostic to species. The genus as defined here, therefore provides a convenient level of description which can be applied to a larger set of sites, but as yet all specimens referred to *Nanowana* are from Riversleigh.

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